Parental energy and fitness costs in birds

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CHAPTER 1

GENERAL INTRODUCTION

Costs of reproduction

The *cost of reproduction* is a concept used with two different meanings in the literature. The first is the collective of resources devoted by a parent animal to the production, growth and protection of its current offspring. In this, more colloquial, sense the energy expenditure of a bird feeding its nestlings has been considered as the energy cost of reproduction.

In an evolutionary sense, the cost of reproduction is defined for iteroparous animals only. Natural selection is expected to maximise the rate of gene propagation (*i.e.*, fitness) of individuals. For iteroparous animals, fitness consists of the contributions of both current and expected future reproduction. Maximisation of fitness with respect to any trait - such as energy allocated to the current offspring - refers to the value of that trait that yields the highest fitness return, while deviations of this (optimal) trait value in either direction should lead to submaximal fitness. This implies that benefits to the current (offspring) component of fitness as a result of an increase in the trait value beyond the optimal value should be more than cancelled by costs to the future (parent) component of fitness. And *vice versa*. These negative correlations between fitness components, or *life history traits*, are (microevolutionary) trade-offs. This forms the theoretical basis for expecting that an animal engaging in reproduction incurs a fitness cost by losing some of its expected future reproduction, the parental *residual reproductive value* (Williams 1966). The reduction in expected future reproduction - for which Trivers (1974) coined the term *parental investment* - benefits the current offspring.

The residual reproductive value is itself composed of a number of components, such as the probability of survival till next breeding, the probability of mating (if survived), the expectation of the number of eggs produced (if mated), etc. Current reproductive effort may entail a fitness cost of reproduction in any of these components. Thus, Trivers' parental investment may - in principle - be composed of multiple fitness costs. Although these fitness costs of reproduction are conceptually distinct from the energy costs of reproduction, it is expected that the two have some biological relationship. This relationship is far from unravelled. If there are multiple fitness costs, one may in fact expect multiple relationships. The relationship between energy turnover of altricial birds and their fitness costs of reproduction are the theme of the present thesis.

There are two approaches to understand fitness costs of reproduction. On the one hand, one may answer the question of why there are costs of reproduction by invoking functional explanations, *i.e.*, by studying fitness consequences of (artificial) variation in (a component of) current reproduction. On the other hand, by studying how costs of reproduction are caused, one may identify ecological and physiological mechanisms that impose fitness costs on the parent.

Evolutionary causes

Functional explanations of costs of reproduction start from optimality models, and aim at showing that a change in one life history trait that increases fitness, *e.g.*, clutch size, is related to a change in another trait that decreases fitness. To establish the existence of a trade-off, variation in one trait has to be manipulated experimentally (Reznick 1985;

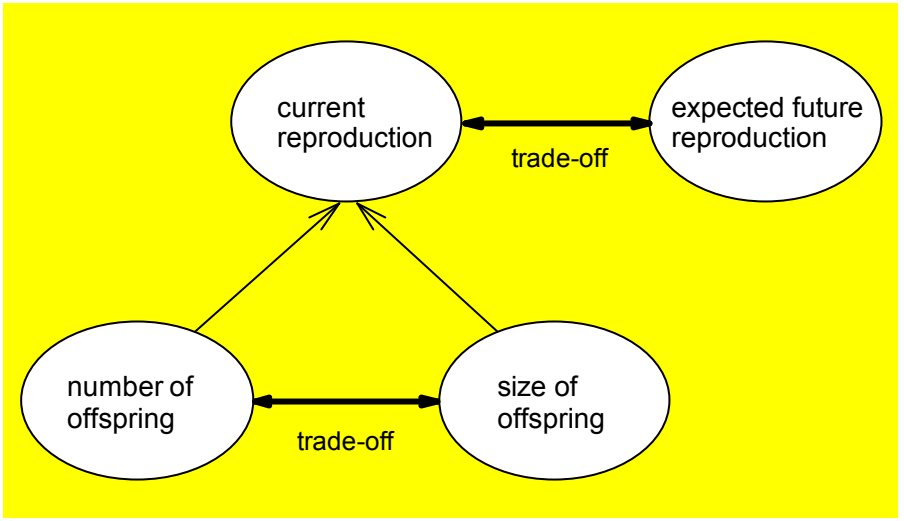

Figure 1. The relation between the two major life history trade-offs in which clutch size, i.e., number of offspring, plays a predominant role.

Partridge & Harvey 1988). One general experimental approach exploits manipulations of current reproduction through manipulation of clutch or brood size (Lessells 1991), and quantification of subsequent reproductive succes of experimental and later broods. Clutch size figures in two major trade-offs (Figure 1; Lessells 1991). The first trade-off concerns the proportion of available resources devoted at one time to reproduction - which is reflected in the clutch size - as oppposed to growth or storage. Growth and storage may benefit the expected future reproduction. The second trade-off, *i.e.*, between number of offspring and fitness of individual offspring, deals with the division of reproductive effort among offspring. The latter trade-off will only be touched upon in this thesis.

The fitness cost of reproduction may find expression in any component of later reproduction. The fitness value of an individual is a function of its age-specific survival and reproduction (Lessells 1991). Consequently, current reproduction may be at the expense of the rate or intensity of future reproduction, as demonstrated for timing (Slagsvold 1984; Hegner & Wingfield 1987; Ten Cate *et al.* 1993), or incidence of subsequent clutches, or both (Tinbergen 1987; Smith *et al.* 1987; Lindén 1988; Møller 1993; Verhulst 1995). Also size (Hegner & Wingfield 1987; Smith *et al.* 1989; Verhulst 1995), and success (Slagsvold 1984; Røskaft 1985) of subsequent clutches, or both (Møller 1993) may be affected. Additionally, costs of reproduction may appear in reduced adult survival rates, often measured as return rates (Askenmo 1979; Bryant 1979; Nur 1984; Dijkstra *et al.* 1990), thereby putting the option of future reproduction at risk (Bell & Koufopanou 1986).

Fitness costs of reproduction are not always obvious from the studies that have been carried out (Harris 1970; De Steven 1980; Boyce & Perrins 1987; Finke *et al.* 1987; Korpimäki 1988; Orell & Koivula 1988; Wheelwright *et al.* 1991; Korpimäki & Rita 1996). Partly, this is because manipulation of clutch or brood size potentially affects two strategic decisions: the trade-off between current and expected future reproduction on the one hand, and the trade-off between offspring number and size on the other hand (Figure 1). If parents adjust the size of the offspring in response to manipulation of their number, parental effort, that is the allocation of resources to reproduction, is not necessarily altered by the manipulation (Lessells 1991, 1993).

As a consequence of this, fitness costs of reproduction can not be established. In addition, negative results in the search for costs of reproduction (*i.e.*, no costs identified) may be due to a limited scope of possibilities that have been examined, namely short-term measurements of reproductive success or incomplete data, *e.g.*, local survival. For short-term measures of reproductive success to be meaningful, it is assumed that they are positively related to reproductive success in the long term (Reeve & Sherman 1993).

Physiological causes

Fitness costs of reproduction may arise through various mechanisms. Both extrinsic, ecological factors, and intrinsic, physiological processes have been suggested to be instrumental in the cost of reproduction phenomenon (Partridge 1992).

Ecological mechanisms are involved mainly in the temporal component of reproduction. Survival costs of reproduction may stem from altered risks of predation or parasitism (Calow 1979; Magnhagen 1992; Partridge 1992) as a consequence of a change in time allocation due to current reproductive activities. Recently, a surge of evidence has become available about positive effects of reproduction on the prevalence of parasites (Festa-Bianchet 1989; Møller 1993; Norris *et al.* 1994; Richner *et al.* 1995). Reproductive costs may further be incurred by negative effects of the duration of the current reproductive attempt on the timing or incidence of a subsequent reproductive attempt (Verhulst 1995), or moult and storage of body reserves to ensure successful migration or overwinter survival.

Physiological mechanisms concern the reallocation of limited resources between reproduction and growth and/or storage. Fitness-related physiological processes may compete directly for limited resources (energy, time, nutrients) within an individual according to the 'principle of allocation' (Calow 1979; Sibly & Calow 1986a). Reproduction may therefore compromise, for instance, parental body condition (Drent & Daan 1980), thereby affecting survival or later reproductive potential (Lima 1986; Houston & McNamara 1993). A reduction in body mass as a consequence of parental effort has been reported for many species (reviews in: Dijkstra *et al.* 1990; Martins & Wright 1993). Two studies have reported a direct association between body mass of reproducing birds and later survival (Nur 1984; Tinbergen, pers. comm.), although this association is not necessarily causal, because both variables were affected by manipulation of brood size. A direct, and causal correlation between adult mass and survival has been shown outside the breeding season only (Marcström & Kenward 1981; Haramis *et al.* 1986).

Parental energy and fitness costs

Daan *et al.* (1990a) have proposed a mechanism for fitness costs of reproduction by hypothesising that the energy cost of reproduction, *i.e.*, the rate of energy expenditure of parents may be instrumental in the trade-off between current and future reproduction. This hypothesis has two implicit assumptions. The first is the energetic reiteration of the individual optimisation hypothesis. Current reproduction is supposed to be adjusted to

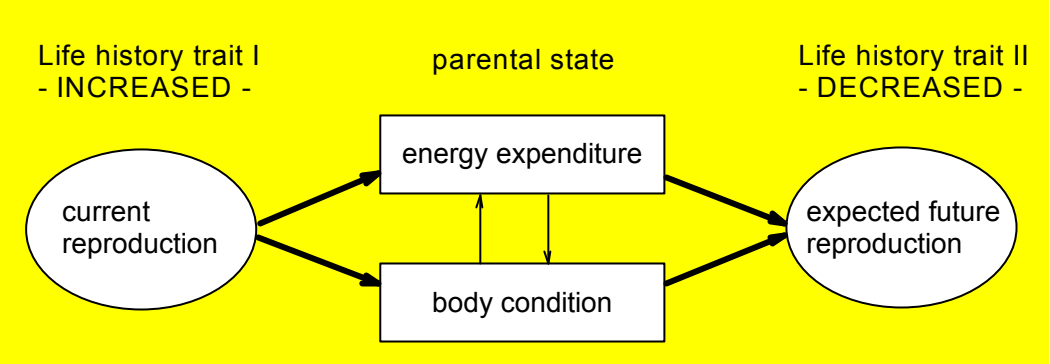

Figure 2. The mechanism proposed by Daan et al. (1990a) through wich involvement in current reproduction is linked to a reduction in later reproduction.

individual circumstances up to a sustainable working level that does not compromise body condition or other risks of life. This working level - in terms of units of basal metabolic rate (BMR) - is expected to be similar across individuals and species (Drent & Daan 1980). The second assumption is that parents indeed adjust their available resources, and thus their energy expenditure, to the manipulated brood size. It remains to be elucidated whether the trade-off between reproduction and parental fitness costs is a consequence of parental energy *per se*, or results from (secondary) effects of the rate of energy expenditure on, *e.g.*, parental body condition. Deterioration of parental body condition may actually be one step in a chain of effects causing fitness costs of reproduction (Figure 2).

The evidence for a causal relationship between parental rates of energy expenditure and future fitness parameters is scant. Few studies have assessed energy costs of reproduction, *i.e.*, a correlation between brood size and parental energy expenditure (Williams 1987; Dijkstra *et al.* 1990; Moreno *et al.* 1995; but see Verhulst 1995), while fitness costs of reproduction have been assessed on the same species, in the same study area, but on a different sample of birds (Dijkstra *et al.* 1990; Verhulst 1995). Therefore, the evidence between parental energy and fitness costs is indirect, and does not necessarily indicate a causal relationship. Also, the derived relationship is qualitative: brood size reductions reduce energy expenditure and fitness costs of parents, and enlargements of brood size increase both energy expenditure and fitness costs. Direct, and quantitative evidence requires associations between individual parental rates of energy expenditure and fitness costs. The single study on Great Tits *Parus major* that meets this requirement, failed to assess systematic positive relationships between the two variables (Verhulst 1995). This scant evidence leaves unanswered to a large extent the intriguing question of whether fitness costs of reproduction directly result from parental rates of energy expenditure. To address this question, several steps have been taken in this thesis.

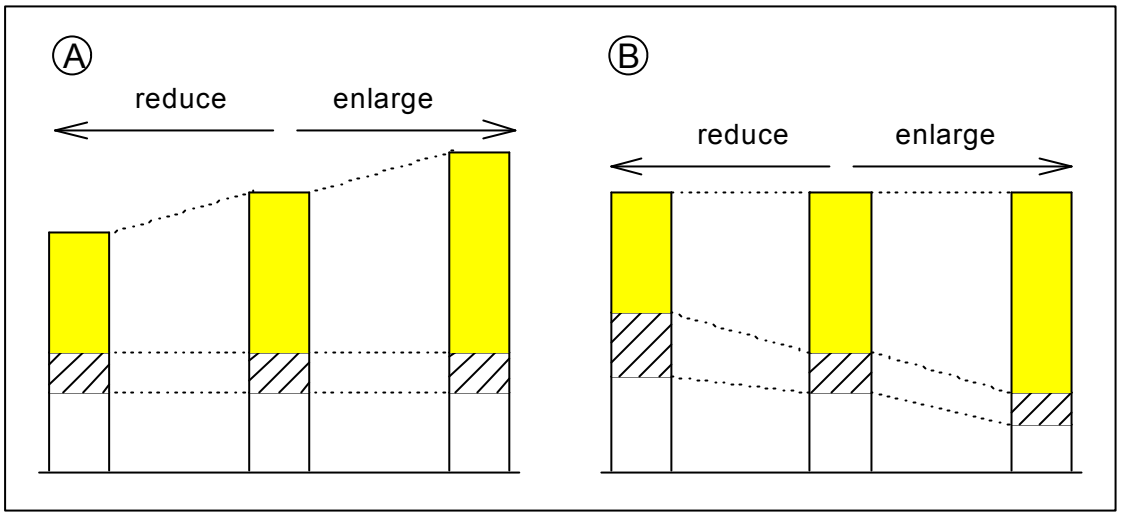

Figure 3. Two strategies of allocation of daily energy expenditure (DEE) to reproduction (shaded area), activity (open area), and maintenance (hatched area) in response to manipulation of reproduction.

OUTLINE OF THE STUDY

First, current reproduction and energy costs to the parents have to be manipulated, and both energy turnover rates and fitness costs of reproduction have to be assessed. Current reproduction is usually manipulated by changing the clutch or brood size. We chose to extend a long-term field study on the European Kestrel *Falco tinnunculus*, where both parental energy metabolism and fitness costs had been estimated previously (Dijkstra 1988). In this species, reduction of brood sizes resulted in increased return rates of the parents to the study area (*local survival*), while enlargement of brood sizes led to decreased return rates of the parents. For local survival, *i.e.*, return rates, to actually reflect global survival, it is assumed that there is no biased emigration from the studied area. To verify that local survival truly reflected global survival, we estimated survival rates from experimental birds recovered dead by the general public (Chapter 2). It turned out that differential mortality of parents did not occur until after several months. This refutes the notion of immediate ecological risks associated with parental effort.

Second, the potential involvement of parental energy expenditure has to be established. Thus, the dependence of parental energy on (manipulated) brood size has to be examined. Parents may respond to manipulation of reproductive energy costs in two ways. One strategy involves a modification of available resources (Figure 3a) by altering foraging decisions (Boggs 1992). A change in the total amount of resources may be achieved simply by adjusting foraging time and effort, or by a change of diet without compromising time or effort, *e.g.*, through selection of food of different quality (*e.g.*, Tinbergen 1981). If the animal is in energetic and nutrient balance, the amount of resources available will be reflected in the parental rates of energy expenditure, which

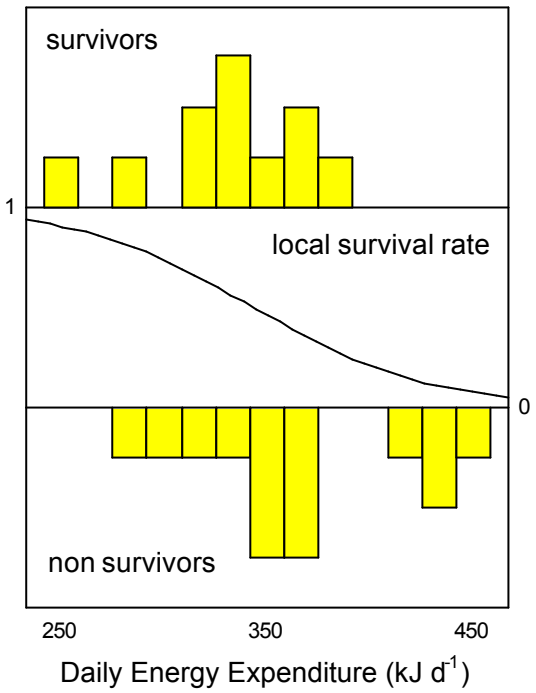

Figure 4. Local survival rate as a function of parental daily energy expenditure (DEE). The upper and lower panels show a frequency distribution of DEE of parents with manipulated broods that were recaptured in the study area during the next breeding season (upper panel), and of parent birds that were not recaptured (lower panel). The middle panel depicts the curve as estimated by the logistic regression of parental local survival rate on DEE.

then provide a simplifying and generalising representation of parental effort. A change in energy expenditure, assessed either by time-energy budgets (TEB) or by turnover of stable istopes (Doubly Labeled Water method, DLW) parallel to experimental changes in brood size has been established in several studies (TEB: Dijkstra *et al.* 1990; DLW: Williams 1987; Moreno *et al.* 1995; Tinbergen pers. comm.).

The other response strategy to manipulation of reproductive effort involves a reallocation of available resources (Figure 3b) by (temporarily) abandoning growth or storage (Kozlowski 1991), or by adjusting maintenance and activity costs, *e.g.*, through body mass or body composition (Daan *et al.* 1989). Impairment of body condition may lead to somatic damage, with either temporary (*exhaustion* Cavé 1968), or permanent effects (*senescence* Partridge 1987; Gustafsson & Pärt 1992), thus causing costs of reproduction. Many studies have shown that manipulation of clutch or brood size differentially affects body mass of parents (reviews in: Dijkstra *et al.* 1990; Martins & Wright 1993), but this result does not necessarily reflect a true reallocation strategy. Two studies have shown that parental energy expenditure appeared unaffected by manipulation of brood size, while reproductive success (*i.e.*, no. of fledglings) was proportional to experimental brood size (Verhulst 1995; J. Wright pers. comm.).

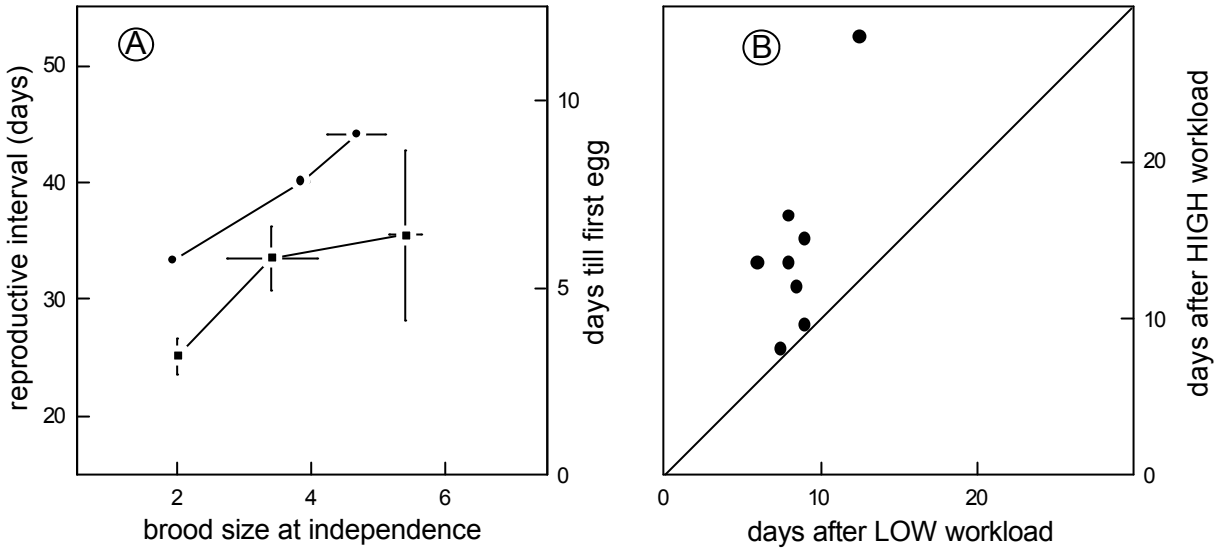

Figure 5. A. Reproductive interval (= days between hatching of experimental brood and first egg of subsequent brood; ●) in relation to final brood size of the experimental brood, or (■) days till first egg of subsequent brood after a forced interval of 50 days. B. Number of days till laying of the first egg of zebra finch pairs after being subjected to a high versus a low workload. The line represents equal number of days.

Energy expenditure of kestrel parents with manipulated brood sizes - previously estimated from time-energy budgets (Dijkstra *et al.* 1990) - was measured with stable isotopes (Chapter 3). Our results confirmed Dijkstra's conclusion that energy expenditure of parents increase with the manipulation, which is in agreement with the first strategy of adjustment of available resources. By identifying the breeding population in the subsequent year, a direct negative association of energy expenditure during reproduction and subsequent (local) survival rates could be established on an individual basis (Figure 4; Chapter 3).

Thus, these experiments with kestrels yielded results that are consistent with the hypothesis that energy expenditure during reproduction is the crucial factor leading to fitness costs. These results, however, do not preclude alternative explanations, such as delayed timing of post-reproductive moult and reduced storage of body reserves. To establish a causal involvement of energy expenditure in fitness costs, it is necessary to manipulate energy expenditure of adult birds also using alternative methods, *e.g.*, through manipulation of activity, or by weights attached to the parent bird (Wright & Cuthill 1990), while the duration of the manipulation is held constant. All methods of manipulation should affect at least one component of fitness negatively, if energy expenditure is crucial.

We aimed at manipulating energy expenditure by manipulating daily activity, outside the context of reproduction, and assess the impact on fitness. These kind of experiments are difficult to conduct in a field situation. Moreover, different types of fitness costs may be involved: timing of consecutive phases in the annual cycle (*e.g.*, moult, storage of body reserves), or survival by ecological risks (*e.g.*, predation) or physiological deterioration. To enable close observation of intermediate processes, a laboratory study was initiated. Fitness can

not be measured in the laboratory, but some components of fitness may be examined on birds in captivity. Although kestrels breed easily in captivity (*e.g.* Meijer 1988), they are rather inactive, and a fair amount of daily activity can at best be achieved by intense training and extravagant time-investment of the experimenter (Masman & Klaassen 1987). We therefore decided to start a series of experiments on Zebra Finches *Taeniopygia guttata*. Zebra finches may produce up to six broods in one year (*e.g.*, Ten Cate 1984). In addition, they are easily trained to respond to variable reward ratios, and thereby can be subjected to variable workloads (A. Kacelnik, pers. comm.).

We started out by asking whether a fitness cost of reproduction could be established by means of brood size manipulations in a laboratory environment (Chapter 4). It turned out that the interval till the next reproduction was a component of fitness affected by experimental brood size. Zebra finches raising experimentally enlarged broods delayed their subsequent reproduction, while zebra finches raising a small brood advanced their subsequent reproduction (Figure 5a).

As in the Kestrel, we next had to verify the potential involvement of parental energy in the cost of reproduction phenomenon. Thus, we established whether zebra finches respond to manipulation of brood size by adjusting their energy expenditure, and whether variation in energy expenditure thus manipulated was related directly to reproductive interval (Chapter 5). Unexpectedly, the energetic response of female zebra finches in the *ad libitum* feeding conditions was - qualitatively - similar to that of the kestrels, while energy expenditure of male parents appeared unaffected by the brood size. Not surprisingly, a direct association between parental energy and timing of the subsequent brood could be shown for female zebra finches only.

The crucial test of the hypothesis that energy turnover is causally involved in the generation of a fitness cost of reproduction consisted of an alternative way of manipulating the energy expenditure of adult birds. We imposed two different workloads on the birds and increased their daily activity by applying a food reward system (Chapter 6). After a workload episode, the birds that had been subjected to a high workload took longer to start their subsequent reproduction than did birds that had been subjected to a low workload (Figure 5b). Thus, manipulation of workload through activity affected the same fitness component that was affected by the brood size manipulation experiment.

The results of the experiments on both kestrels and zebra finches are in agreement with the hypothesis that parental energy turnover rate is instrumental in fitness costs of reproduction. Other results, however, such as the reduction in body mass during parental care that is increased in parents raising enlarged broods, while parents of reduced brood loose less weight, are symptoms of a strategy in which less energy is allocated to maintenance in response to manipulation of brood size. These findings do not contradict the hypothesis, but may point at the interference of, *e.g.*, body condition in the mechanism that causes fitness costs. We therefore examined the vitality of the immune system, *i.c.*, an antigen-specific antibody response, of zebra finches (Chapter 7).

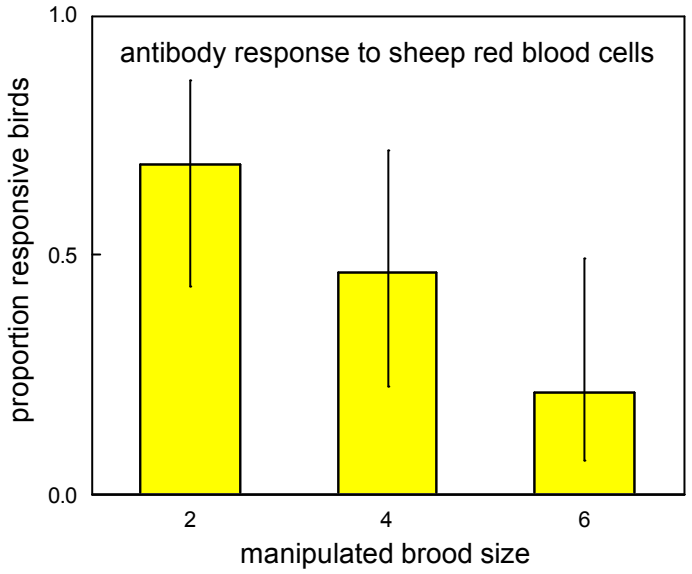

Figure 6. Proportion of zebra finches producing haemagglutinating antibodies against sheep red blood cells as a function of reproductive status. Non-breeding and non-working birds all responded.

Immunocompetence is one aspect of body condition in a broad sense that can be related directly to a fitness component, *i.e.*, risk of (parasitic) infection, thus risk of death. Both experimental manipulation of parental energy (*i.c.*, brood size and workload) affected negatively the responsiveness to the alien antigen, sheep red blood cells (Figure 6). Surprisingly, responsiveness was related neither to energy expenditure of the birds, nor to body mass. A reduction of the vitality of the immune system thus seems yet another mechanism potentially conveying costs of reproduction.

In the workload experiment, we were amazed to find that higher workloads actually induced slightly lower, rather than increased rates of energy expenditure. Instead of an increase in energy expenditure in response to increased demands - either imposed by brood size, or by activity - zebra finches appear to follow a reallocation strategy, or a mixed strategy. Body condition, *i.c.*, body mass of parent birds was affected in every experiment in this thesis. Adjustment of body mass may indeed contribute considerably to stabilising the energy budget. To study the role of body mass, we reconstructed the allocation of energy, and the role of body mass therein, to activity and inactive behaviour (Chapter 8). Compensation for increased energy expenditure due to increased activity was achieved by a major reduction of energy expenditure during rest (Figure 7) - a reduction far more than can be explained by mass reduction alone. Apparently, when faced with increased energetic demands, birds cut down on other processes, as already indicated by the reduction in immunocompetence. The key role of energetic costs causing fitness costs of reproduction may therefore be attributed tentatively to a simultaneous reduction of energy allocated to maintenance processes

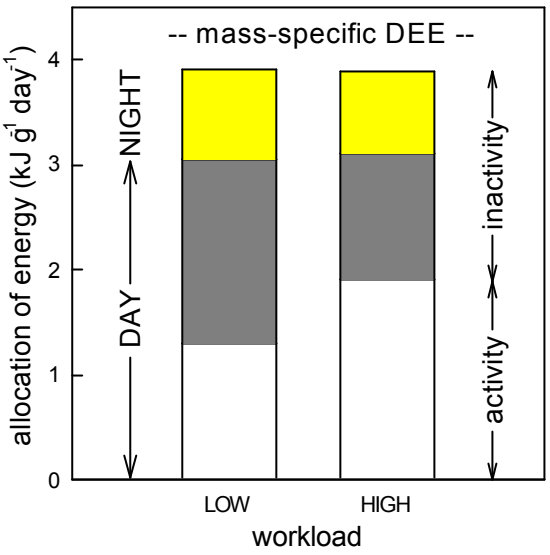

Figure 7. Allocation of mass-specific daily energy expenditure (DEE) to night (shaded area), hopping activity (open area) and diurnal inactive behaviour (hatched area).

rather than to a change in the overall energy budget alone. The nature of these maintenance processes remains to be revealed.